PROC. BIOL. SOC. WASH.
91(1), 1978, pp. 74–84

A REVISION OF THE GENUS *PSAMMORYCTIDES* (OLIGOCHAETA: TUBIFICIDAE) IN NORTH AMERICA

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The genus *Psammoryctes* was erected by Vejdovský (1876) for *Saenuris barbata* Grube, 1861; the name was amended to *Psammoryctides* by Hrabě (1964) due to prior use of the original. Since Hrabě's (1950) revision of the genus, there have been few changes in the parameters of the generic definition. The genus is found in Europe and North America, with seven or eight European species (depending on the acceptance or rejection of synonymies). Species of *Psammoryctides* are recent additions to the North American fauna. Three species previously described and reported are *P. californianus* Brinkhurst, 1965, *P. minutus* Brinkhurst, 1965, and *P. curvisetosus* Brinkhurst and Cook, 1966.

Examinations of serial sections and whole-mount specimens of *P. convolutus* n. sp. (described herein) led me to a reexamination of the North American species and a subsequent reevaluation of their relationships based on the characteristics of the efferent portion of the male ducts. Subgenera are proposed to indicate the close kinship among the North American species and their separation from their European cogeners. Partially dissected specimens of *P. californianus* were made available to me by D. R. Spencer of NUS Corporation. Type-series of the three previously described species were borrowed from the U.S. National Museum of Natural History, Smithsonian Institution.

Types of *Psammoryctides californianus*, *P. minutus*, and *P. curvisetosus* were in unsatisfactory condition. Dissected and whole-mount specimens were in a macerating mounting medium. Cells were dissolved, tissues fused, and the bases of many setae partly obscured. Configurations of the male ducts were accurately determined only by phase microscopy at magnifications to 1,000 diameters. One paratype of *P. minutus*, infiltrated with air that had entered under the coverslip, was of little worth.

Genus Psammoryctides Hrabě, 1964

Hrabě (1964) described the distal portion of the male efferent system of *P. barbatus*, the generic type, as illustrated by Vejdovský (1876), to have 4 parts: a small atrium, a narrowed proximal portion of the ejaculatory duct, a distal swollen portion of the ejaculatory duct, and a penial bulbus with a penis. Brinkhurst's (1971) definition of the genus added only that the penes are eversible and bear sheaths.

North American species possess a fifth part: a thin-walled portion of the ejaculatory duct distal to the swollen part and proximal to the penis. This character was apparently unnoticed by Brinkhurst (1965) in his description of *Psammoryctides californianus* and *P. minutus*. Because these two species and *P. convolutus* n. sp. form such a closely related complex independent from the European species of *Psammoryctides*, I propose that subgenera be erected for the separation of the North American and European forms. The generic definition is amended to read as follows:

> Male efferent duct with a somewhat globular atrium and compact prostate gland; ejaculatory duct with swollen, glandular portion separated from atrium by a narrow tubular portion. Eversible penes with thin cuticular penis sheaths. Genital setae frequently present. No coelomocytes.

The reclassification of the genus is as follows:

Subgenus *Psammoryctides* Hrabě, 1964. New Status.

Swollen glandular portion of ejaculatory duct terminating in a penis. Subgeneric type: *Psammoryctides* (*Psammoryctides*) *barbata* (Grube, 1861). Distribution: Europe.

Subgenus *Spencerius*, subgen. nov.

Ejaculatory duct comprised of 3 portions: proximal thin-walled tube, median thick-walled glandular portion, distal thin-walled tube terminating in a penis. Subgeneric type: *Psammoryctides* (*Spencerius*) *californianus* Brinkhurst, 1965. Distribution: North America.

Etymology.—Named for Douglas R. Spencer, who provided specimens of *P. californianus* that led to this study.

Psammoryctides (*Spencerius*) *californianus* Brinkhurst, 1965
Fig. 1

Description.—Length 7.5–12 mm. Forty–seventy segments. Anterior dorsal bundles with 2–5 finely serrate hair setae, 372–459 μm long, and 2–4 pectinate setae, 75–93 μm long; pectinates slightly palmate, with fine intermediate teeth. Posterior dorsal bundles with 1–2 hairs, 312–336 μm long, and 1–2 pectinate setae, 72–79 μm long, similar in shape to those located anteriorly. Anterior ventral setae all bifid crochets, 3–4 per bundle, 81–86 μm long, distal tooth longer and thinner than proximal. Posterior ventral setae 2–3 per bundle, 63–72 μm long, distal tooth longer and thinner than proximal.

Male reproductive tract with all structures paired. Vasa deferentia of

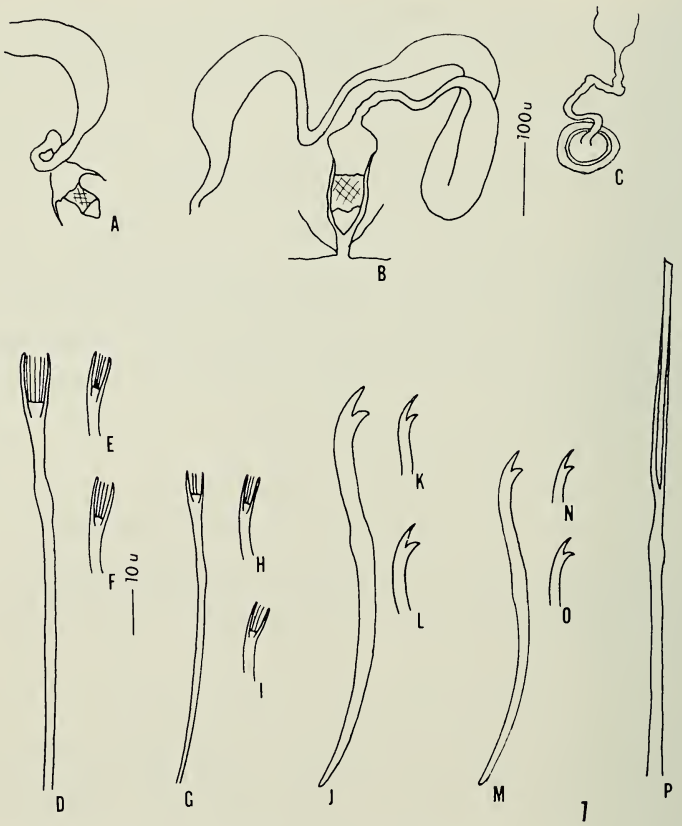

Fig. 1. *Psammoryctides californianus.* A–C, Male duct: A, Holotype; B, Michigan; C, New York. D–F, Anterior dorsal setae: D, Holotype; E, Michigan; F, New York. G–I, Posterior dorsal setae: G, Holotype; H, Michigan; I, New York. J–L, Anterior ventral setae: J, Holotype; K, Michigan; L, New York. M–O, Posterior ventral setae: M, Holotype; N, Michigan; O, New York. P, Spermathecal seta.

undetermined length, 21 μm diameter. Atrium 39–43 μm wide, 119 μm long. Prostate gland 71 μm wide, 214 μm long, location of junction with atrium undetermined. Ejaculatory duct with thin-walled proximal portion 24 μm diameter, thick-walled median portion 45–52 μm diameter, and thin-walled distal portion 11–24 μm diameter. Penes 33–47 μm wide, 95 μm long; thin cuticular penis sheath 33–47 μm wide, 42–55 μm long, encircling penis medially. Spermethecal ampulla globular, 165 μm diameter; duct 215 μm long. Spermathecal setae one per bundle ventrally in X, 117–125 μm long; teeth fused to form a groove.

Specimens examined.—Holotype (USNM 32662). California: Santa Clara

Co., Coyote Creek (No paratypes).—D. R. Spencer coll.: Michigan: St. Clair Co., Black River, 1 specimen. New York: Cayuga Lake, 1 specimen.

Remarks.—Examination of the holotype and specimens from the Spencer collection revealed a distal narrowing of the ejaculatory duct. Spencer's material differed from the holotype only in some measurements of the genitalia, an exaggeration in lengths of the teeth of ventral setae, and in the slightly smaller distal end of pectinate setae. The above redescription is based on characters from the holotype and more recently collected material. A summer breeding season for the species is indicated by sexual maturity in California and Michigan specimens collected in May and New York material in August.

Psammoryctides (*Spencerius*) *minutus* Brinkhurst, 1965. New Status.
Fig. 2

Description.—Length 7–12 mm. Forty–eighty-four segments. Anterior dorsal bundles with 3–5 finely serrate hair setae, 331–493 μm long, and 3–5 pectinate setae, 90–118 μm long; pectinates varying in form from having the lateral teeth parallel and somewhat palmate to sigmoid setae with the distal tooth thinner and slightly longer than the proximal; setal variation without any segmental sequence, often in the same bundle. Hair setae absent from posterior bundles (usually from XIII–XVI, although one specimen with hairs to XXVIII). Posterior dorsal setae all bifid crochets, 1–2 per bundle, 80–109 μm long, distal tooth shorter and thinner. Anterior ventral setae 4–6 per bundle, 71–85 μm long, teeth subequal to distal longer. Posterior ventrals 2 per bundle, 56–75 μm long, the distal tooth shorter and thinner than the proximal.

Male reproductive tract with all structures paired. Vas deferens of undetermined length, 18 μm diameter, ciliated. Atrium 80 μm wide, 163 μm long. Prostate not observed. Ejaculatory duct composed of 3 sections: proximal narrow tube, 160 μm long, 20 μm diameter; medial swollen portion, 275–300 μm long, 70–85 μm diameter; distal narrow portion 165 μm long, 20–28 μm diameter. Cuticular penis sheath thin, 117–140 μm long, 85–120 μm basal diameter, 54–70 μm distal diameter.

Penial setae 3–4 per bundle, 147 μm long, 8 μm wide. Spermathecal ampullae ovoid, 215 μm wide, 400 μm long; ducts 35 μm wide, 285 μm long. Spermatozeugmata up to 380 μm long, 70 μm wide, narrowing at one end.

Specimens examined.—Holotype (USNM 32639): Lake Tahoe, California/Nevada.—Paratypes (USNM 32640): Same locality, 6 specimens.

Remarks.—Brinkhurst (1971) judged this species to be a *species incerta sedis* possibly from some uncertainty concerning the distal narrowing of the ejaculatory duct. His dissected specimens clearly showed the similarity of the ejaculatory duct to that of the other North American species of

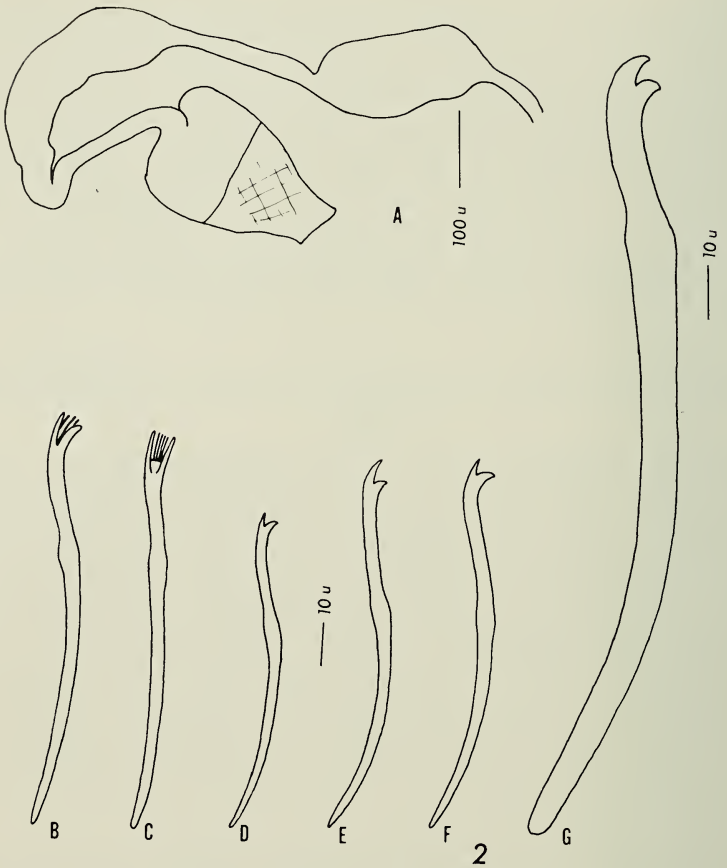

Fig. 2. *Psammoryctides minutus*. A, Male duct; B, C, Anterior dorsal setae; D, Posterior dorsal seta; E, Anterior ventral seta; F, Posterior ventral seta; G, Penial seta.

Psammoryctides (Fig. 2A). I therefore recommend that it be removed from the *species incerta sedis* status and reinstated as a valid species of *Psammoryctides*.

Psammoryctides (*Spencerius*) *convolutus* n. sp.
Fig. 3

Holotype.—NMNH 54463. Louisiana: Ascension Parish; swamp at Sorrento Oil Dome; 4.1 km ESE Sorrento, 30°10′18″N, 90°47′05″W, 27 September 1976, M. S. Loden.—Paratypes: NMNH 54464. Same locality and date, 4 specimens. LSU 1828; same locality and date, 5 specimens (1 serially sectioned). Additional collections: LSU 1826. Mexico: Hidalgo; 2 km

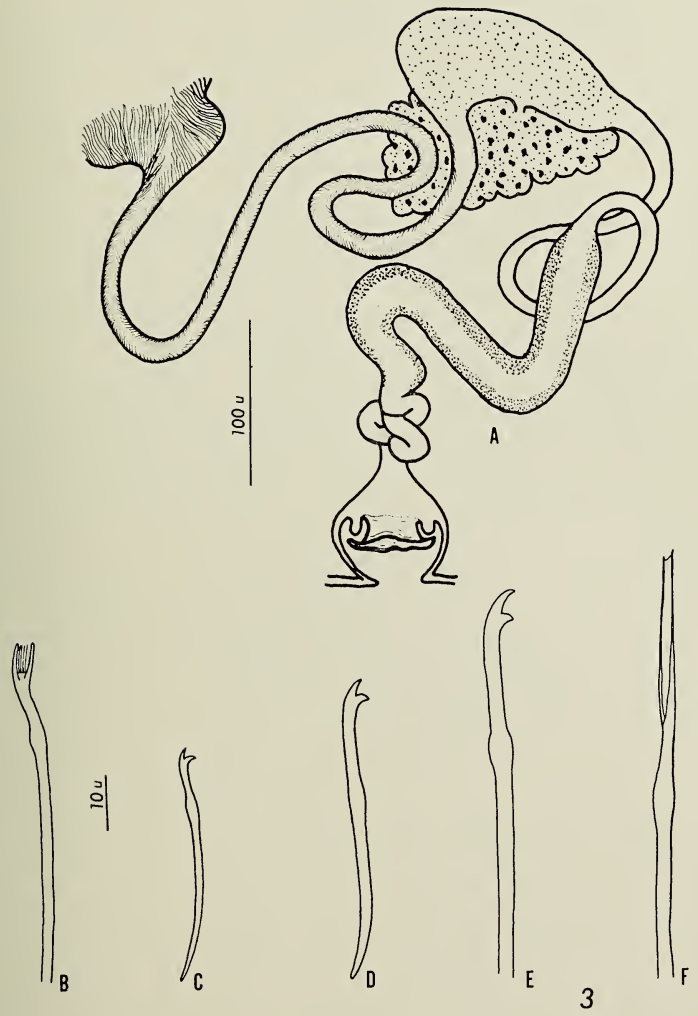

Fig. 3. *Psammoryctides convolutus.* A, Male duct; B, Anterior dorsal seta; C, Posterior dorsal seta; D, Anterior ventral seta; E, Posterior ventral seta; F, Spermathecal seta.

NE Metepec. (Central Plateau), 6 May 1974, M. A. Tidwell, 1 specimen. LSU 1827. Florida: Collier Co.; Canal and marsh along US 41; 1.0 mi E Paolita, 1 November 1976, W. J. Harman and M. S. Loden, 6 specimens.

Etymology.—"*convolvere*" L. "to roll together." Refers to the convoluted distal end of the ejaculatory duct.

Description.—Sixty-six to 88 segments. Length 10–25 mm (preserved). Diameter at anterior end 0.2 mm, 0.26 mm at segment XI, 0.2 mm at pos-

terior end. Prostomium rounded, as long as width at peristomial junction. Clitellum extending from 10/11 to XII/2.

Anterior dorsal bundles consisting of hair setae and pectinate setae to XIII or XIV (occasionally to XV), posteriorly only bifid crochet setae. Hairs 1–3 per bundle, serrated or non-serrated, 117–175 μm in II, reaching maximum size in VI–VIII of up to 485 μm long, 2.2 μm basal diameter, decreasing in length posteriorly to 90–100 μm maximum length in their posteriormost bundles. Pectinate setae 1–3 per bundle, 39–58 μm long, 2.0 μm thick; lateral teeth parallel, 5–8 μm long, the proximal tooth slightly longer; intermediate teeth fine, numerous. Posterior dorsal setae 1–3 per bundle (usually 2), 44–51 μm long, 1.7 μm thick; teeth equally long or distal slightly shorter; proximal tooth slightly thicker; nodulus distal.

Anterior ventral setae bifid, 3–4 per bundle, 39–58 μm long, ca. 2 μm thick; teeth equally long or distal slightly longer; teeth equally thick; nodulus distal. Beyond the clitellum ventral setae becoming gradually thicker and longer; those of pre-periproct region 1–2 per bundle, up to 81 μm long, 3.6 μm thick; distal tooth more than twice as long as proximal, and thicker; nodulus distal.

Male genital system with all structures paired. A conical male funnel on septum 10/11. Vas deferens ca. 550 μm long, 20 μm diameter, lined with cilia throughout its length. Atrium 90 μm long, 40 μm wide, joined at the median concave surface by a compact prostate, 120 μm long, 80 μm maximum width. Ejaculatory duct in three portions: a thin-walled proximal portion ca. 100 μm long, 23 μm diameter; a thick-walled glandular central portion 90 μm long, 30 μm diameter; a convoluted thin-walled distal portion 11 μm diameter, length undetermined, but occupying a space of 40 μm. Cuticular penis sheath 20 μm long, 27 μm basal diameter, with a reflexed head 51 μm diameter. Penis sac ovoid, 70 μm maximum diameter. Male pores ventrolateral on XI, in the setal plane. Spermathecae paired in segment X. Ampullae globular, 85 μm diameter; duct 130 μm long, 20 μm diameter. Spermatozeugmata ca. 155 μm long; basal expansion present or absent, varying in diameter from 15–45 μm; distal end tapered. Modified spermathecal setae in X, adjacent to spermathecal pores, one per bundle, 84–105 μm long. Teeth elongate, fused, forming a groove.

Remarks.—Psammoryctides convolutus was the most common oligochaete among the roots of emergent aquatic vegetation where more than 100 specimens were collected over a period of 3 months. Swamp habitats ranged from mixed hardwood and bald cypress to a pure cypress stand. The swamp substrate was a fine, organic mud. Additional worms of this species were found in samples from the Florida everglades, again in a fine, organic mud substrate. A single specimen was present in a collection from a roadside ditch in east-central Mexico. Sexually mature worms were collected in Louisiana from September to December, with the greatest number found

in November. *Psammoryctides convolutus* likely has a continuous distribution throughout the swamps of the Gulf coastal plain of the southeastern United States and eastern Mexico.

Peloscolex curvisetosus (Brinkhurst and Cook, 1966), comb. nov.
Fig. 4

Brinkhurst and Cook (1966) mentioned in their description that the swelling of the ejaculatory duct just proximal to the penis of *P. curvisetosus* was "not so marked as in some species." The diameter of the narrow portion of the ejaculatory duct in the holotype was 32 μm, and that of the swollen part was 44 μm; therefore the swelling was weak. The "swollen" part in the holotype (Fig. 1A; Brinkhurst and Cook, 1966, Fig. 6M) overlies the integument and associated body wall musculature; the tissues had fused somewhat due to the mounting medium, possibly creating a more exaggerated expansion than was actually present. The swelling of this portion of the ejaculatory duct is likely a normal expansion prior to its termination in a penis; this feature is almost identical to those illustrated by Brinkhurst (1971) for many tubificid species not having the expended ejaculatory duct characteristic of *Psammoryctides*.

The penis sheath of *P. curvisetosus* was described by Brinkhurst (1971) as being scarcely thicker than the body wall cuticle. Due to the vertical position of the penis on the slide, no detectible thickening of the cuticle to form a penis sheath was seen. A second sexually mature individual of *P. curvisetosus* (M. S. Loden coll.) also showed no penis sheath of a greater thickness than integumentary cuticle.

The configuration of the male duct of *P. curvisetosus* was almost identical to that of *Peloscolex tenuis* Hrabě, 1931. Both had a prostate joining a curved atrium on its anterior concave surface, and long, narrow ejaculatory ducts. They differ in that in *P. tenuis* a distinct penis sheath and body wall papillae are present and genital setae are lacking, while in *P. curvisetosus* there is no distinct penis sheath, papillae and hair setae are lacking, and spermathecal setae are present. Thickened, recurved posterior ventral setae and hair setae are characteristic of *P. tenuis* (Hrabě, 1931, 1964) and *P. curvisetosus* (Fig. 1F, G).

Because of similarity in male reproductive anatomy of *Psammoryctides curvisetosus* to *Peloscolex tenuis*, and therefore its agreement with Brinkhurst's (1971) definition of *Peloscolex*, I can see no alternative to a generic transfer of this species. A papillate or thickened body wall, an earlier requirement for the placement of a species into *Peloscolex* (Hrabě, 1964), is no longer regarded as diagnostic (Pickavance and Cook, 1971; Erséus, 1976).

In addition to the type-locality (Lake Erie), *P. curvisetosus* has been

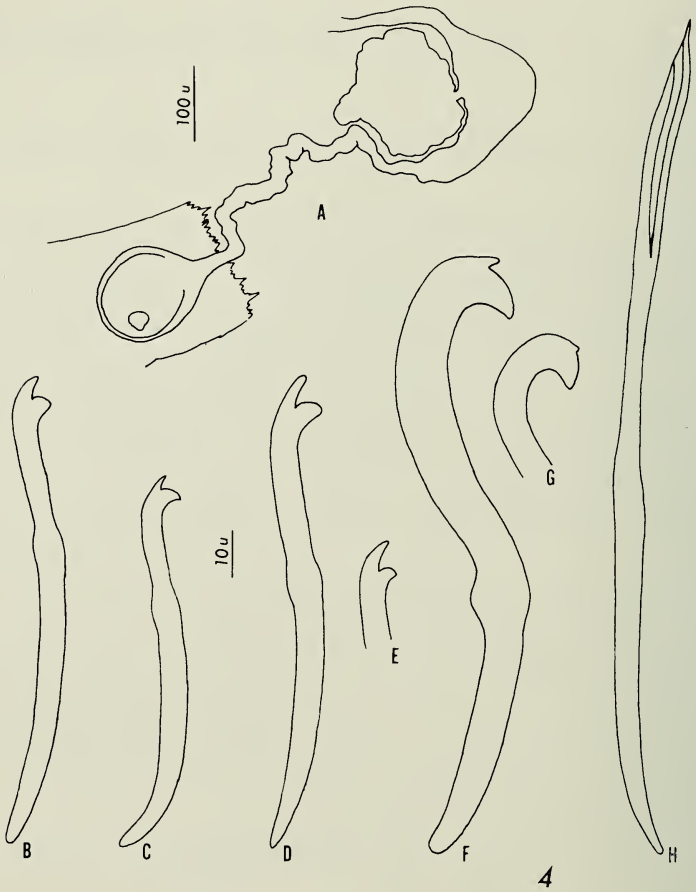

Fig. 4. *Peloscolex curvisetosus*, holotype. A, Male duct; B, Anterior dorsal seta; C, Posterior dorsal seta; D, E, (Alabama), Anterior ventral setae; F, G, (Alabama), Posterior ventral setae; H, Spermathecal seta.

collected from Pennsylvania (LSU 1868), Indiana (LSU 1876), North Carolina (LSU 1878), and Alabama (LSU 1877), all from small rocky streams. Sexual maturity in specimens outside the Great Lakes has been observed only in winter collections. Some slight variations in the shape of the setae were found in specimens from the various localities (Fig. 1).

Discussion

The 3 North American species of *Psammoryctides* differ in both genital and somatic setal characters (summarized in Table 1). *Psammoryctides minutus* is unique in having penial setae and lacking spermathecal setae.

Table 1. Summation of some characters for *Psammoryctides* species of the subgenus *Spencerius*. +: present; −: absent.

	P. (S.) *californianus*	*P.* (S.) *minutus*	*P.* (S.) *convolutus*
Penial setae	−	+	−
Spermathecal setae	+	−	+
Posterior hair setae	+	−	−
Enlarged posterior ventral setae	−	−	+
Pectinate posterior dorsal setae	+	−	−

The anterior dorsal setae of the 3 species bear some similarity: all 3 have pectinate setae with rather long, parallel lateral teeth, and intermediate teeth arising from a portion of the seta some distance from the bases of lateral teeth. Posterior dorsal setae differ among the three; *P. californianus* has hair setae throughout the length of the worm and has posterior pectinates of a shape similar to that of anterior pectinates. Posterior dorsal bundles of *P. minutus* and *P. convolutus* lack hair setae; the posterior dorsal crochets of *P. minutus* have the distal tooth shorter and thinner than the proximal and those of *P. convolutus* have the teeth subequal and the proximal tooth only slightly thicker.

Anterior ventral setae of the 3 species are similar: those of *P. californianus* have the distal tooth longer and thinner than the proximal; *P. minutus* often has the distal tooth longer, but with the teeth equally thick; and *P. convolutus* has subequal teeth of equal thickness. The posterior ventrals of the 3 species differ considerably: those of *P. convolutus* are thicker and longer than the ventral setae of the anterior segments, and with a long, thick distal tooth; *P. californianus* has posterior ventrals of a smaller size than its anterior ventrals, and a distal tooth longer, but thinner than the proximal; in *P. minutus* the posterior ventrals are generally shorter than the anterior ventrals, with a thinner, shorter distal tooth.

Except for the differences in measurements and the location of the sheaths on the penes, the male genitalia of the 3 species are almost idential; *P. convolutus* differs from the others in that the distal portion of the ejaculatory duct is convoluted. The penis sheath of *P. convolutus* (Fig. 3A) is located at the base of the penis and is reflexed at the head. That of *P. californianus* (Fig. 1A, B, C) is located medially on the penis and is simple. The penis sheath location of *P. minutus* was difficult to determine from the dissected type-specimens, but appeared not to be basal (Fig. 2A); it was a simple structure having much greater dimensions than that of *P. californianus*.

It is probable that additional species of *Psammoryctides* will be found in North America. One specimen of an immature tubificid (M. S. Loden

coll.) with pectinate setae of the same form as those described for the 3 known species probably represents a fourth species.

Acknowledgments

I wish to thank Dr. Walter J. Harman for his advice and encouragement. Specimens from the U.S. National Museum of Natural History were kindly lent by Dr. Marian H. Pettibone, Curator of Worms. Special thanks are due to Douglas R. Spencer for allowing me to examine his specimens.

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